

Seasonal Dynamics and Community Structure of Helminths of Spotted Sunfish, *Lepomis miniatus* (Osteichthyes: Centrarchidae) from an Oligohaline Estuary in Southeastern Louisiana, U.S.A.

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ABSTRACT: The seasonal dynamics of the helminth community of the spotted sunfish *Lepomis miniatus* Warren, 1992, from an oligohaline estuary were investigated over a 1-yr period. From 26 May 1991 to 25 May 1992, 7 helminth species (3 Trematoda, 2 Nematoda, 2 Acanthocephala) were recovered from the gastrointestinal tracts of 200 specimens of *L. miniatus*. The parasite community of this host was dominated by the trematodes *Barbulostomum cupuloris* and *Genarchella* sp. Both helminths were recruited and matured in this host throughout the year, but their times of peak abundance differed. *Barbulostomum cupuloris* was most abundant in February–May, whereas *Genarchella* sp. abundance peaked in November–February. *Camallanus oxycephalus* and *Leptorhynchoides thecatus* showed a similar pattern of seasonal abundance, which was highest in May–August for both species. The remaining 3 helminths, *Crepidostomum cornutum*, *Neoechinorhyncus cylindricus*, and *Spinitectus carolini*, were too rare to detect annual patterns of abundance. Infra- and component community diversity and richness did not vary seasonally, but infracommunity predictability was greatest in February–May.

KEY WORDS: parasite, helminth, seasonal dynamics, Centrarchidae, *Lepomis miniatus*, estuary, infracommunity, component community, community, Louisiana, USA.

Seasonal fluctuations in prevalence and abundance are common in many helminths of freshwater fishes (Eure, 1976; Chubb, 1979), but the mechanisms influencing seasonality are sometimes difficult to identify. Chubb (1979) concluded that, in general, seasonal patterns of occurrence of helminths are often species-specific and dependent upon: 1) how the helminth invades its host, 2) helminth growth and maturation, 3) accumulation of eggs, and 4) loss of gravid worms. Abiotic factors such as temperature may also affect the seasonal cycles of many helminths (Chappell, 1969; Anderson, 1974, 1976; Eure, 1976; Granath and Esch, 1983a–c).

Seasonal patterns of abundance of the helminths of centrarchid fishes in freshwater environments have been previously examined (McDaniel and Bailey, 1974; Cloutman, 1975; Eure, 1976), but studies addressing temporal variability of helminths in nongame centrarchids are lacking. More importantly, the helminth fauna of centrarchid fishes inhabiting estuarine environments has received little attention. Fiorillo and Font (1996) characterized the helminth communities of 4 species of *Lepomis* from a low-salinity estuary and showed that the compound

community of centrarchid fishes in brackish water habitats differed from that of centrarchids in freshwater environments.

In this study, we examined the seasonal pattern of abundance of all helminths that utilize *Lepomis miniatus* Warren, 1992, as a definitive host in an oligohaline estuary. In addition, we used community measures to investigate seasonal fluctuations in the infracommunity and component community structure of *L. miniatus*.

Materials and Methods

From 26 May 1991 to 25 May 1992, 200 specimens of *L. miniatus* were collected from a 1.1-km section of a canal along Interstate Highway 55 located between the south bank of Pass Manchac and Ruddock, Louisiana, in St. John the Baptist Parish. This man-made canal is part of the oligohaline Lake Pontchartrain-Lake Maurepas estuary located in southeastern Louisiana. The salinity of this large estuary ranges from 0 ppt at the western shore of Lake Maurepas to 15 ppt at the eastern shore of Lake Pontchartrain, but at our study site, salinity never exceeded 3 ppt. Temporal variation in water temperature was determined using a Datasonde 3[®] water quality data logger (Hydrolab Corporation, Austin, Texas) located near our study site at the Turtle Cove Research Station on Pass Manchac, Louisiana.

Our 1-yr collection period was divided into 4 periods of equal duration. Forty-five specimens were collected during the May–August period (May 26–August 26), 53 during August–November (August 27–November 26), and 51 each during the November–February

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(November 27–February 26) and February–May (February 27–May 25) periods. There was a minimum interval of 1 mo between collections made in different time periods. All hosts were captured by angling or with hoop nets and crab traps baited with cat food and checked at 1–2-day intervals. The sex and standard length of each fish were recorded, and the stomach, pyloric ceca, and intestinal tract were examined for adult helminths. Trematodes were fixed in Berland's solution (9 parts acetic acid, 1 part 37% formaldehyde) and stored in AFA (alcohol-formalin-acetic acid). Nematodes were fixed in Berland's solution and placed in glycerine alcohol. After acanthocephalans were refrigerated in distilled water overnight to extrude the proboscis, several small holes were made in the body wall with fine dissecting pins prior to fixation in AFA. Trematodes and acanthocephalans were stained with Semichon's carmine, dehydrated in a graded alcohol series, cleared in xylene, and mounted in Permount®. Nematodes were cleared and mounted in glycerine jelly.

The influence of host body size (standard length, mm) on helminth abundance and community attributes was examined with Pearson's correlations. The prevalence and abundance (Bush et al., 1997) of all helminths were calculated overall and for each time period. Helminth abundance data were square root transformed prior to statistical analyses. Seasonal patterns of helminth prevalence and abundance were analyzed with chi-square tests and ANOVA or ANCOVA, respectively.

Because *Barbulostomum cupuloris* and *Genarchella* sp. were the most abundant helminths in the component community of this host, a contingency table analysis was used to examine for concurrent patterns of infection. Based on gonadal development, these 2 trematodes were assigned to 1 of 3 developmental stages. Specimens of *B. cupuloris* were scored as immature, mature, or gravid, and specimens of *Genarchella* sp. were categorized as nongravid, gravid, or heavily gravid. Immature specimens of *B. cupuloris* were defined as individuals having incomplete gonadal development and lacking vitellaria. Mature worms were characterized by complete gonadal development, but egg production had not yet begun. Individuals with eggs and highly packed vitellaria were classified as gravid. Specimens of *Genarchella* sp. that possessed incompletely developed gonads and lacked eggs were classified as nongravid. Gravid worms were characterized by completely formed testes and ovary, but the lobes of the vitellaria of these specimens were not clearly distinct. The uteri of these gravid specimens contained eggs, but they were only slightly convoluted and well confined within the intercecal space. Heavily gravid worms were characterized by vitellaria possessing distinct lobes. The uteri of heavily gravid specimens were distended with eggs, highly convoluted, and typically extended laterally beyond the ceca. The seasonal patterns of abundance of these developmental stages were examined with ANOVA or ANCOVA. Voucher specimens of all species and developmental stages have been deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland, under

USNPC accession numbers 84483–84485, 84489, 84490, 88573 and 88574.

Overall and within each time period, Brillouins's diversity index, which is appropriate for fully censused communities (Pielou, 1977), was used to estimate infracommunity and component community diversity. Seasonal mean infracommunity diversity was compared using ANOVA. As a measure of infracommunity predictability, Renkonen's coefficient of similarity was used to determine overall and within-season infracommunity similarity. Seasonal mean infracommunity similarity was compared using ANOVA, and in addition, Renkonen's coefficient of similarity was used to compare the component community of this host among time periods.

Results

Seven helminth species (3 Trematoda, 2 Nematoda, 2 Acanthocephala), *Barbulostomum cupuloris*, *Genarchella* sp., *Crepidostomum cornutum*, *Camallanus oxycephalus*, *Spinitectus carolini*, *Leptorhynchoides thecatus*, and *Neoechinorhynchus cylindratus*, were recovered from the alimentary tracts of 200 *L. miniatus* (standard length in mm: $\bar{x} \pm \text{SE}$, range; 96.9 ± 0.91 , 68–126) collected from the Lake Pontchartrain-Lake Maurepas estuary. Host body size differed significantly among seasons (ANOVA, $P < 0.05$). The largest hosts were collected in the May–August time period (104 ± 1.51 , 84.5–126). Host body size decreased through August–November (101 ± 1.3 , 83.1–121) and November–February (99.1 ± 1.42 , 78.1–118) and was lowest in February–May (84.0 ± 1.6 , 68.0–109). Water temperature in this oligohaline estuary was highest in July and gradually decreased to its lowest value in January (Fig. 1).

With the exception of *C. cornutum*, whose abundance was greater in female hosts ($\bar{x} \pm \text{SE}$, range; 0.12 ± 0.04 , 0–3) (male hosts, 0.02 ± 0.02 , 0–2) (t -test, $P < 0.05$), there were no sex-related differences in helminth abundance. In addition, only *C. cornutum* ($\chi^2 = 5.137$, $P < 0.05$) and *L. thecatus* ($\chi^2 = 10.442$, $P < 0.05$) showed host sex-related differences in prevalence, and as a result, both sexes were pooled for subsequent statistical analyses.

Only the abundance of *B. cupuloris* displayed a statistically significant relationship with host body size (overall, $r = -0.254$, $P < 0.01$). In addition, no statistically significant correlations between host size and helminth species abundance were found within each collecting period ($P > 0.05$).

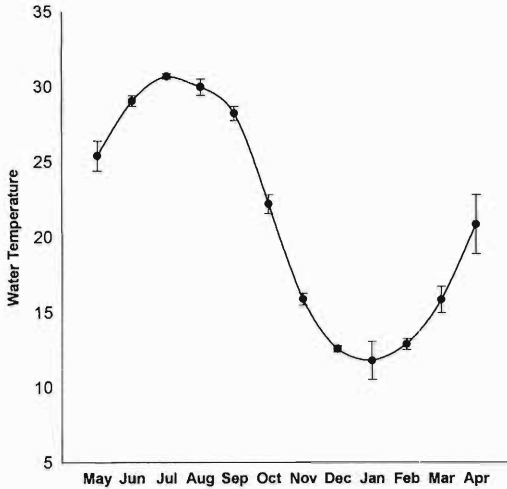


Figure 1. Mean monthly water temperature (°C) in Lake Pontchartrain-Lake Maurepas estuary (1992–1995). Vertical bars represent ± 1 standard error of the mean.

Helminth seasonal dynamics

Prevalence of *B. cupuloris* differed significantly among time periods ($\chi^2 = 28.98$, $P < 0.05$). Thirty-six percent of hosts examined in May–August harbored at least 1 specimen. Prevalence increased to 40% in August–November and 41% in November–February before reaching 82% in February–May. Irrespective of developmental stage, *B. cupuloris* was most abundant in February–May (8.8 ± 1.28 , 0–37), displaying an 82% increase in abundance from the previous November–February time period (1.6 ± 0.47 , 0–20) and a considerable decrease in the subsequent May–August period (1.1 ± 0.4 , 0–15) (2-way ANCOVA, $P < 0.05$) (Fig. 2a). Abundance also differed with respect to developmental stage (2-way ANCOVA, $P < 0.05$), but no interaction effect was found (2-way ANCOVA, $P > 0.05$). Mature specimens were most abundant (1.5 ± 0.24 , 0–21), followed by gravid specimens (1.4 ± 0.22 , 0–18) and immature worms (0.6 ± 0.13 , 0–14). In addition, each developmental stage of *B. cupuloris* showed a statistically significant seasonal cycle of abundance (ANCOVA, $P < 0.05$ for each stage). The abundance of each stage was lowest in May–August, remained low in the following August–November and November–February periods, and reached maximum abundance in February–May (Fig. 2a).

Thirteen percent of hosts in May–August

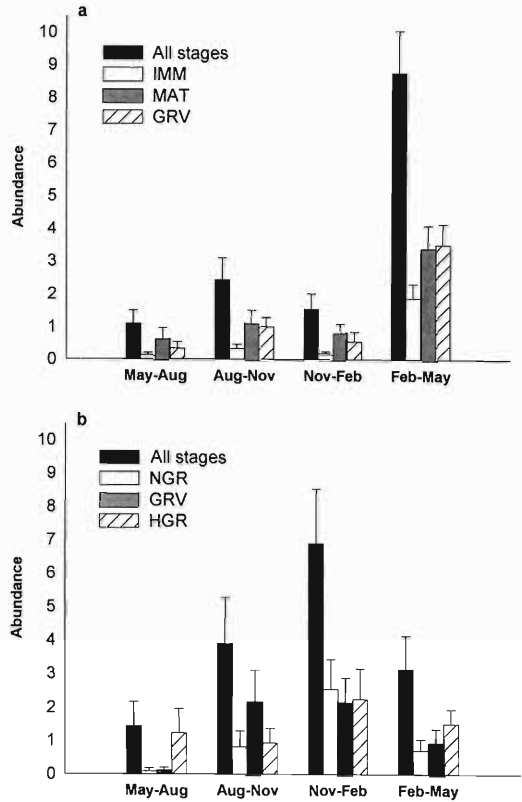


Figure 2. Seasonal abundances of (a) *Barbulosom cupuloris* (all stages) and each developmental stage (IMM, immature; MAT, mature; GRV, gravid); (b) *Genarchella* sp. (all stages) and each developmental stage (NGR, nongravid; GRV, gravid; HGR, heavily gravid). Vertical bars represent ± 1 standard error of the mean.

were infected with *Genarchella* sp. Prevalence increased through August–November (34%) to reach a peak in November–February (49%) before decreasing in February–May (39%) ($\chi^2 = 13.69$, $P < 0.05$). *Genarchella* sp. was most abundant in November–February (6.9 ± 1.62 , 0–41), a 44% increase from the previous August–November time period (3.9 ± 1.39 , 0–43) and showed its lowest abundance in May–August (1.4 ± 0.74 , 0–23) (2-way ANOVA, $P < 0.05$) (Fig. 2b). Overall, there was no difference in abundance among developmental stages and no interaction effect (2-way ANOVA, $P > 0.05$). Both nongravid and gravid worms showed statistically significant seasonal cycles of abundance (ANOVA, $P < 0.05$ for each stage). Non-gravid and gravid worms were most abundant in November–February (2.5 ± 0.89 , 0–27) and Au-

gust–November (2.2 ± 0.94 , 0–41), respectively, and least abundant in May–August (nongravid: 0.09 ± 0.09 , 0–4; gravid: 0.1 ± 0.08 , 0–3) (Fig. 2b).

Camallanus oxycephalus was most prevalent and abundant in May–August (36%) (0.7 ± 0.26 , 0–11). Prevalence and abundance declined throughout the year and were lowest in February–May (10%) (0.1 ± 0.05 , 0–2), ($\chi^2 = 12.888$, $P < 0.05$) (ANOVA, $P < 0.01$), respectively (Table 1, Fig. 3). Prevalence of *L. thecatus* did not change seasonally ($\chi^2 = 5.278$, $P > 0.05$) (Table 1), but its abundance did vary among time periods and peaked in May–August (0.6 ± 0.19 , 0–5) (ANOVA, $P < 0.05$) (Fig. 3). *Crepidostomum cornutum*, *S. carolini*, and *N. cylindratus* were uncommon (prevalence of each, $< 7\%$), and too few individuals (abundance of each, < 0.1) were recovered to determine seasonal patterns of prevalence and abundance (Table 1).

Parasite abundance (overall: 8.2 ± 0.8 , 0–56) differed significantly among time periods (ANCOVA, $P < 0.05$). Abundance was lowest in May–August (4.0 ± 0.87 , 0–26), increased during August–November (7.3 ± 1.66 , 0–53) and November–February (8.5 ± 1.54 , 0–45), and reached its highest value during February–May (12.8 ± 1.81 , 0–56).

Infracommunity analysis

Overall, host body size was correlated with infracommunity diversity ($r = 0.18$, $P < 0.05$), but this relationship was not significant within time periods. The most diverse infracommunity was found in November–February (1.294 ± 0.197 , 0.0–4.14), whereas in February–May, infracommunity diversity was lowest (0.689 ± 0.136 , 0.0–3.35). The remaining 2 time periods, May–August and August–November, showed intermediate levels of infracommunity diversity (0.889 ± 0.151 , 0.0–3.40 and 0.959 ± 0.185 , 0.0–4.01, respectively). However, infracommunity diversity did not differ significantly among time periods (ANCOVA, $P > 0.05$). Overall infracommunity diversity was 0.963 ± 0.087 (0.0–4.14).

Both overall and within time periods, host body size did not influence infracommunity species richness. Helminth richness was lowest in May–August (1.244 ± 0.143 , 0–4) and increased in August–November (1.302 ± 0.139 , 0–3) and November–February (1.353 ± 0.096 ,

0–3). Infracommunity richness was greatest in February–May (1.549 ± 0.113 , 0–3). However, infracommunity species richness did not differ significantly among time periods (ANOVA, $P > 0.05$). Overall infracommunity species richness was 1.365 ± 0.062 (0–4). Infracommunity predictability differed significantly among time periods (ANOVA, $P < 0.001$). Infracommunity similarity was greatest in February–May (0.56 ± 0.01 , 0–1) and lowest in May–August (0.22 ± 0.01 , 0–1). In August–November and November–February, infracommunity similarity values were intermediate (0.31 ± 0.01 , 0–1 and 0.34 ± 0.01 , 0–1, respectively). Overall infracommunity similarity was low (0.31 ± 0.003 , 0–1).

Component community analysis

The trematodes *B. cupuloris* and *Genarchella* sp. were the most prevalent and abundant helminths and dominated the component community of *Lepomis miniatus* (Table 1). *Barbulostomum cupuloris* was most prevalent (50%), and although *Genarchella* sp. was recovered from fewer hosts (35%), its overall abundance (3.9 ± 0.64 , 0–43) did not differ significantly from that of *B. cupuloris* (3.5 ± 0.46 , 0–37) (*t*-test, $P > 0.05$). Although together these 2 trematodes accounted for 1,485 of the total 1,662 worms recovered during this study (89%), no significant association was found between them with respect to concurrent patterns of infection ($\chi^2 = 0.032$, $P > 0.05$). The nematode *C. oxycephalus* was recovered from 24% of hosts examined, but its abundance was low (0.4 ± 0.08 , 0–11). The remaining 4 helminth species showed low prevalence and abundance and, together with *C. oxycephalus*, represented only 11% of the total helminth specimens recovered (Table 1).

Component community diversity was low (0.47). It was greatest in February–May (1.16), progressively declined through May–August (0.63) and August–November (0.45), and was lowest in November–February (0.34). Component community species richness changed slightly over the year. Six helminth species were recovered during May–August, August–November, and November–February, whereas 7 helminth species were found in February–May (Table 1). The trematode *C. cornutum* and the acanthocephalan *N. cylindratus* were the only helminths not found in all 4 time periods (Table 1). Component community comparisons among time periods were made using Renkonen's co-

Table 1. Overall and seasonal prevalence, abundance, and range of helminths of *Lepomis miniatus*.

Helminth	May–Aug., <i>n</i> = 45	Aug.–Nov., <i>n</i> = 53	Nov.–Feb., <i>n</i> = 51	Feb.–May, <i>n</i> = 51	Overall, <i>n</i> = 200
<i>Barbulostomum cupuloris</i> (Ramsey, 1965)	36, 1.1 ± 0.4, 0–15	40, 2.4 ± 0.67, 0–23	41, 1.6 ± 0.47, 0–20	82, 8.8 ± 1.28, 0–37	50, 3.5 ± 0.46, 0–37
<i>Genarchella</i> sp.	13, 1.4 ± 0.74, 0–23	34, 3.9 ± 1.39, 0–43	49, 6.9 ± 1.62, 0–41	39, 3.1 ± 1.00, 0–36	35, 3.9 ± 0.64, 0–43
<i>Crepidostomum cornutum</i> (Stafford, 1904)	0, 0	11, 0.1 ± 0.05, 0–2	2, 0.06 ± 0.06, 0–3	8, 0.1 ± 0.06, 0–2	6, 0.08 ± 0.07, 0–3
<i>Camallanus oxycephalus</i> (Ward and Magath, 1916)	36, 0.7 ± 0.26, 0–11	34, 0.6 ± 0.14, 0–5	18, 0.4 ± 0.13, 0–3	10, 0.1 ± 0.05, 0–2	24, 0.4 ± 0.08, 0–11
<i>Spinitectus carolini</i> (Holl, 1928)	2, 0.02 ± 0.02, 0–2	2, 0.04 ± 0.04, 0–2	2, 0.04 ± 0.04, 0–2	1, 0.04 ± 0.04, 0–2	2, 0.04 ± 0.02, 0–2
<i>Leptorhynchoides thecatus</i> (Kostylew, 1924)	24, 0.6 ± 0.19, 0–5	9, 0.09 ± 0.04, 0–1	20, 0.3 ± 0.11, 0–3	12, 0.1 ± 0.05, 0–1	16, 0.3 ± 0.05, 0–5
<i>Neoechinorhynchus cylindricus</i> (Van Cleave, 1919)	13, 0.3 ± 0.13, 0–5	0, 0	0, 0	2, 0.06 ± 0.06, 0–3	3.5, 0.08 ± 0.03, 0–5

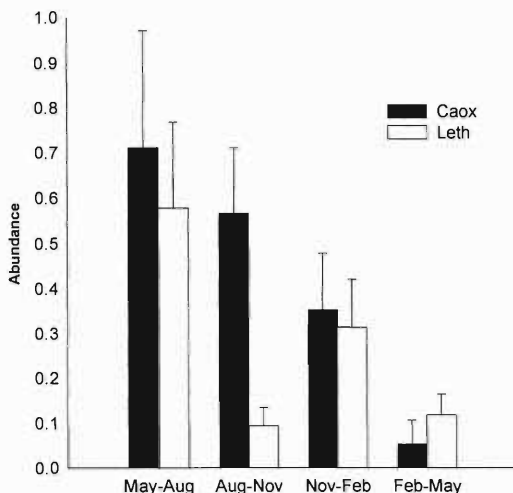


Figure 3. Seasonal abundance of *Camallanus oxycephalus* (Caox) and *Leptorhynchoides thecatus* (Leth). Vertical bars represent ± 1 standard error of the mean.

efficient of similarity. Mean seasonal component community similarity was 0.53 ± 0.058 , $0.41-0.77$. The helminth community of *L. miniatus* in August–November and November–February showed the greatest similarity (0.77), whereas the May–August and November–February communities were least similar (0.45). The remaining comparisons are shown in Table 2.

Discussion

The species composition, richness, and diversity of the helminth community of *L. miniatus* were similar throughout the year. Species-specific and overall abundance of these helminths, infracommunity similarity, and host body size did vary somewhat with season. The trematodes *B. cupuloris*, described from *L. miniatus* (as *Lepomis punctatus* (Valenciennes, 1831)) collected within our study site (Ramsey, 1965), and *Genarchella* sp. were the most prevalent and abundant helminths recovered in this study. These parasites have been reported only in estuarine centrarchid fishes (Fiorillo and Font, 1996), in which they showed distinct seasonal cycles of prevalence and abundance.

Barbulostomum cupuloris was the only helminth to show, possibly as a result of an ontogenetic shift in diet, a significant relationship with host body size. However, the influence of host size was removed statistically from the subsequent seasonal abundance analysis. As a re-

Table 2. Renkonen's coefficients of component community similarity of helminths of *Lepomis miniatus* between paired time periods.

	Aug.–Nov.	Nov.–Feb.	Feb.–May
May–Aug.	0.46	0.41	0.46
Aug.–Nov.		0.77	0.62
Nov.–Feb.			0.45

sult, the nature of the observed seasonal patterns of this and all other helminth species is biological and not a result of changes in host demographics.

Seasonal dynamics of helminth infections

Conditions were optimal for the recruitment and maturation of *B. cupuloris* in February–May, when prevalence was greatest, and each developmental stage of this worm displayed maximum abundance. Following that period, the abundance of each developmental stage and the overall prevalence declined to their lowest values (Fig. 2a). Overall, most *B. cupuloris* specimens recovered were mature or gravid. These data suggest that *B. cupuloris* matures quickly after recruitment. Immature, mature, and gravid specimens were recovered in all 4 collecting periods, indicating that recruitment and egg production occurred throughout the year, irrespective of water temperature. Because of south Louisiana's near-subtropical climate, seasonal changes in water temperature are not extreme (Fig. 1). Although water temperature does not affect egg production in *B. cupuloris*, temperature can influence timing and rate of cercarial production and dispersal (Chappell, 1969; review in Chubb, 1979) and the seasonal abundance of first or second intermediate hosts (Fernandez and Esch, 1991a, b). It is likely that both factors interact to affect the seasonal abundance of *B. cupuloris* in its definitive host.

Similarly, water temperature did not affect recruitment and maturation of *Genarchella* sp. in *L. miniatus*. As with *B. cupuloris*, all 3 developmental stages of *Genarchella* sp. were found throughout the year, but this helminth showed a more gradual increase in recruitment, which peaked in November–February (Fig. 2b). At that time of year, many gravid worms were also recovered. The seasonal cycles of *Genarchella* sp. and *B. cupuloris* were asynchronous. Unlike *B. cupuloris*, which showed maximum prevalence

and abundance in February–May, *Genarchella* sp. was more common and numerous in November–February (Fig. 2a, b). However, as in *B. cupuloris*, the seasonal cycle of *Genarchella* sp. in *L. miniatus* may be linked to the seasonal dynamics of cercarial production and dispersal and to the abundance of the intermediate host.

The life cycles of *B. cupuloris* and *Genarchella* sp. are not known but are probably dependent on brackish water food webs for successful transmission (Ramsey, 1965; Fiorillo and Font, 1996). The lack of a concurrent pattern of infection, as well as the apparent asynchrony in the seasonal cycles of these trematodes, suggest that they do not share the same intermediate hosts.

A qualitative analysis of the gut contents of *L. miniatus* in May–August showed that this centrarchid preyed primarily on amphipods (Fiorillo and Font, 1996). Similarly, Levine (1980) reported that amphipods made up 75% of all prey items of *L. miniatus* in the Lake Pontchartrain–Lake Maurepas estuary. However, Fiorillo and Font (1996) showed that in May–August, both helminths were much more prevalent and abundant in redear sunfish *Lepomis microlophus* (Günther, 1859), a host well known for its specialized diet of bivalves and other mollusks (Wilburn, 1969; Lauder, 1983). In this estuary, Levine (1980) reported that the diet of *L. microlophus* consisted primarily of molluscs, but some amphipods were also taken. A qualitative gut analysis in May–August showed that *L. microlophus* preyed on amphipods, isopods, and bivalves (Fiorillo and Font, 1996). These data suggest that amphipods and bivalves may represent potential second intermediate hosts for these 2 trematodes.

The nematode *C. oxycephalus* was most prevalent and abundant in May–August. Prevalence and abundance declined through the subsequent time periods and were lowest in February–May. It is likely that the seasonal dynamics of *C. oxycephalus* in this estuary are dependent on the seasonal abundance of its copepod intermediate host as shown by Stromberg and Crites (1975) in Lake Erie. Unfortunately, we have no data on the seasonal dynamics of copepod populations in the Lake Pontchartrain–Lake Maurepas estuary to support this assumption, but, generally, zooplankton populations in temperate climates increase in the summer months (Pennak, 1989). Although in our study *C. oxycephalus* abun-

dance was low, we did recover gravid specimens, suggesting that *L. miniatus* is a suitable host for this nematode.

As in *C. oxycephalus*, abundance of *L. thecatus* was low, but this acanthocephalan did show a seasonal cycle of abundance that peaked in May–August. Fiorillo and Font (1996) showed that, in this estuary, *L. thecatus* was much more prevalent and abundant in redear sunfish, *L. microlophus*, and *C. oxycephalus* occurred more frequently in bluegill, *L. macrochirus* Rafinesque, 1819, suggesting that *L. miniatus* is a suitable rather than a required host for these helminths. Leong and Holmes (1981) suggested that, within its environment, the seasonal cycle of a helminth is mostly determined by its seasonal dynamics within its most common host in which the parasite can become reproductive (required host). Therefore, the seasonal cycles of *L. thecatus* and *C. oxycephalus* in *L. miniatus* may not be indicative of the seasonal pattern found in *L. microlophus* and *L. macrochirus*, respectively. Too few specimens of the remaining 3 helminth species were found to determine seasonal cycles of prevalence and abundance, but all are common parasites of centrarchids and other fishes from freshwater environments (see Hoffman, 1967) (Table 1).

Mostly because of increases in abundance of *B. cupuloris* and *Genarchella* sp. (Fig. 2a, b), the overall parasite abundance was greatest in February–May. That time of year is generally associated with an increase in the feeding activity of fishes in Louisiana as water temperature begins to rise (Fig. 1) and many centrarchid species approach the reproductive season (Carlander, 1977). Many invertebrate potential intermediate hosts also show seasonal changes in density, with abundance peaks in early spring (Heard, 1982). Seasonal dynamics of invertebrate intermediate hosts, coupled with seasonal variation in feeding rates and diet of *L. miniatus*, may play an important role in determining the seasonal cycles of abundance of these helminths.

Infracommunity structure

Kennedy (1990) characterized the helminth community of freshwater fishes as depauperate and isolationist. The infracommunity of *L. miniatus* displayed both characteristics. Infracommunities were characterized by a lack of helminth interactions, were species-poor, and included a small number of worms. Consequently,

overall mean infracommunity diversity and species richness of *L. miniatus* were low, similar to other freshwater fishes (Kennedy et al., 1986).

Most fish display indeterminate growth (Wooten, 1990), so that body size is often highly correlated with age (Ricker, 1979; Swales, 1986). In the present study, larger hosts harbored a more diverse infracommunity. This was probably because of greater exposure time, which may increase the probability of these hosts being colonized by the less common helminth species. Cloutman (1975) noted a similar relationship between age and helminth diversity in largemouth bass, *Micropterus salmoides* (Lacépède, 1802).

Seasonality did not affect infracommunity diversity and species richness. With the exception of *C. cornutum* and *N. cylindricus*, all remaining helminths were recovered in all time periods, suggesting that the larval forms of the majority of these helminths are capable of colonizing *L. miniatus* year-round. However, the proportion of infected intermediate hosts, as shown by Fernandez and Esch (1991a, b), may have changed seasonally, resulting in the discrete cycles of abundance shown by some of these helminths.

Overall, the infracommunity structure of *L. miniatus* was not highly predictable, suggesting that each infracommunity represented a random subset of the parasites found in the component community of this host. Poulin (1997) noted that low infracommunity predictability is also a characteristic of isolationist communities, because helminth interactions, which often result in more predictably structured assemblages, are lacking.

Infracommunity predictability did differ among time periods. Infracommunity structure was most and least predictable in February–May and May–August, respectively. In February–May, increases in prevalence and abundance of *B. cupuloris* were largely responsible for the greatest degree of infracommunity similarity, whereas reductions in prevalence and abundance of this trematode, along with *Genarchella* sp., may have contributed to low infracommunity predictability in the following season. The greater predictability in February–May suggests that larval helminths are more prevalent in their intermediate hosts during that time of year so that the probability of individual hosts acquiring a similar suite of parasites is greater.

Component community structure

The trematodes *B. cupuloris* and *Genarchella* sp. were the dominant species in the component

community of *L. punctatus* and accounted for the majority of all worms recovered during this year-long study. These helminths are not found in freshwater centrarchids but have been reported from other *Lepomis* spp. in the Lake Pontchartrain-Lake Maurepas estuary (Fiorillo and Font, 1996). Ramsey (1965) noted that *B. cupuloris* was replaced by the closely related *Homalometron armatum* (MacCallum, 1895) in centrarchid hosts collected in freshwater ponds located near this estuary. In this estuary, *B. cupuloris* and *Genarchella* sp. are more prevalent and abundant in *L. microlophus* (Fiorillo and Font, 1996), suggesting that *L. miniatus* is a suitable but not a required host for these trematodes (Leong and Holmes, 1981). However, the specificity of *B. cupuloris* and *Genarchella* sp. for estuarine hosts reaffirms the importance of ecological associations to the component community structure of *L. miniatus*.

The remaining 5 helminths recovered from *L. miniatus* are common parasites of freshwater centrarchid fishes (see Hoffman, 1967). Although mature forms were found in *L. miniatus*, these helminths showed low prevalence and abundance (Table 1). However, all 5 species were more prevalent and abundant in other *Lepomis* spp. from this estuary (Fiorillo and Font, 1996). These patterns suggest that *L. miniatus* is a suitable host for these helminths (Leong and Holmes, 1981) but that their occurrence in *L. miniatus* may represent accidental infections.

Component community diversity was low and similar to that of other freshwater fishes (Kennedy et al., 1986). Qualitatively, component diversity varied seasonally and was greatest in February–May when *B. cupuloris* and *Genarchella* sp. occurred frequently and abundances were high. The component community of this host in August–November and November–February was most similar. In those time periods, most of the helminths recovered displayed similar measures of prevalence and abundance (Table 1), resulting in a greater degree of similarity.

Overall, the helminth species composition of *L. miniatus* was similar to that of other centrarchid hosts in this estuary (see Fiorillo and Font, 1996). All helminths found in the present study were also recovered in *L. macrochirus* and, with the exception of *C. cornutum*, in *L. megalotis*. However, compared to *L. miniatus*, species richness was much lower in *L. microlophus*. Dietary differences between and among hosts may ac-

count for this result (Bell and Burt, 1991), but unequal sampling effort may have biased this pattern (see Levine, 1980; Fiorillo and Font, 1996, for diet analyses).

Further studies are necessary to determine the life cycles of *B. cupuloris* and *Genarchella* sp. Knowledge of the intermediate hosts of these trematodes and their seasonal patterns of abundance, as well as of temporal changes in the trophic interactions of intermediate hosts and fish, is essential to our understanding of the mechanisms that determine the seasonal dynamics of these helminths and the parasite community structure of this centrarchid host. In addition, a better understanding of these life cycles and seasonal patterns of incidence and abundance would further elucidate the importance of *L. miniatus* to the circulation of these helminths in this estuarine ecosystem.

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